

HYPSOCEPHALUS ATLANTICUS, A NEW GENUS AND
SPECIES OF LUTJANID FISH FROM
MARINE EOCENE LIMESTONES OF
NORTHERN FLORIDA¹

By CAMM SWIFT² AND BROOKS ELLWOOD³

ABSTRACT: A single neurocranium (and a few other bone fragments) representing an undescribed genus and species of hoplopagrine lutjanid was discovered in solution caverns in Eocene limestones in Jackson County, Florida. It is quite distinct from the only living member of this subfamily, *Hoplopagrus guntheri*, known from southern Baja California to Panama in the eastern Pacific Ocean. The Hoplopagrinae are distinct from other lutjanids in possessing: 1) strong, blunt, conical teeth on the premaxillary, dentary, vomer and palatine; 2) a largely vertical posterior face on the basioccipital; 3) exoccipital condylar surfaces which fail to meet in the midline; 4) relatively small otic capsules; and 5) a strong, globular, ventral swelling near the posterior end of the parasphenoid, apparently serving as a brace for the upper pharyngeals.

In Eocene times when the sea was deeper and warmer, the hoplopagrine lutjanids were present near the northern Gulf of Mexico of today. For some reason the group disappeared on the Atlantic side but persisted in the eastern Pacific Ocean. This subfamily is not known outside the New World.

The snappers, family Lutjanidae, are common, worldwide fishes in tropical and subtropical marine shore waters. A few species enter estuaries, and several others are little known species occurring about hard substrate in deep water. Despite this recent abundance, snappers are scarce in the fossil record, and only two records could be found for fossil snappers in North America (Gregory, 1930; Jordan and Gilbert, 1919). Elsewhere in the world three genera (*Caesio*, *Lednevia*, *Lutjanus*) have been recorded from Eocene and Miocene deposits of Europe, and *Lutjanus* has been noted from the Miocene of Australia (Romer, 1966). Summary works on fossil fishes by Smith-Woodward (1901), Casier (1966), Danil'chenko (1967), and Lehman (1966) mention no lutjanid genera. Six other doubtful fossil records for the family are based on otoliths (Weiler, 1968), five from the London Clay and one of *Lutjanus* from Borneo.

¹EDITORIAL COMMITTEE FOR THIS CONTRIBUTION

William A. Gosline
Robert J. Lavenberg
Stanley H. Weitzman

²Associate Curator of Fishes, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

³Graduate School of Oceanography, University of Rhode Island, Kingston, Rhode Island 02881.

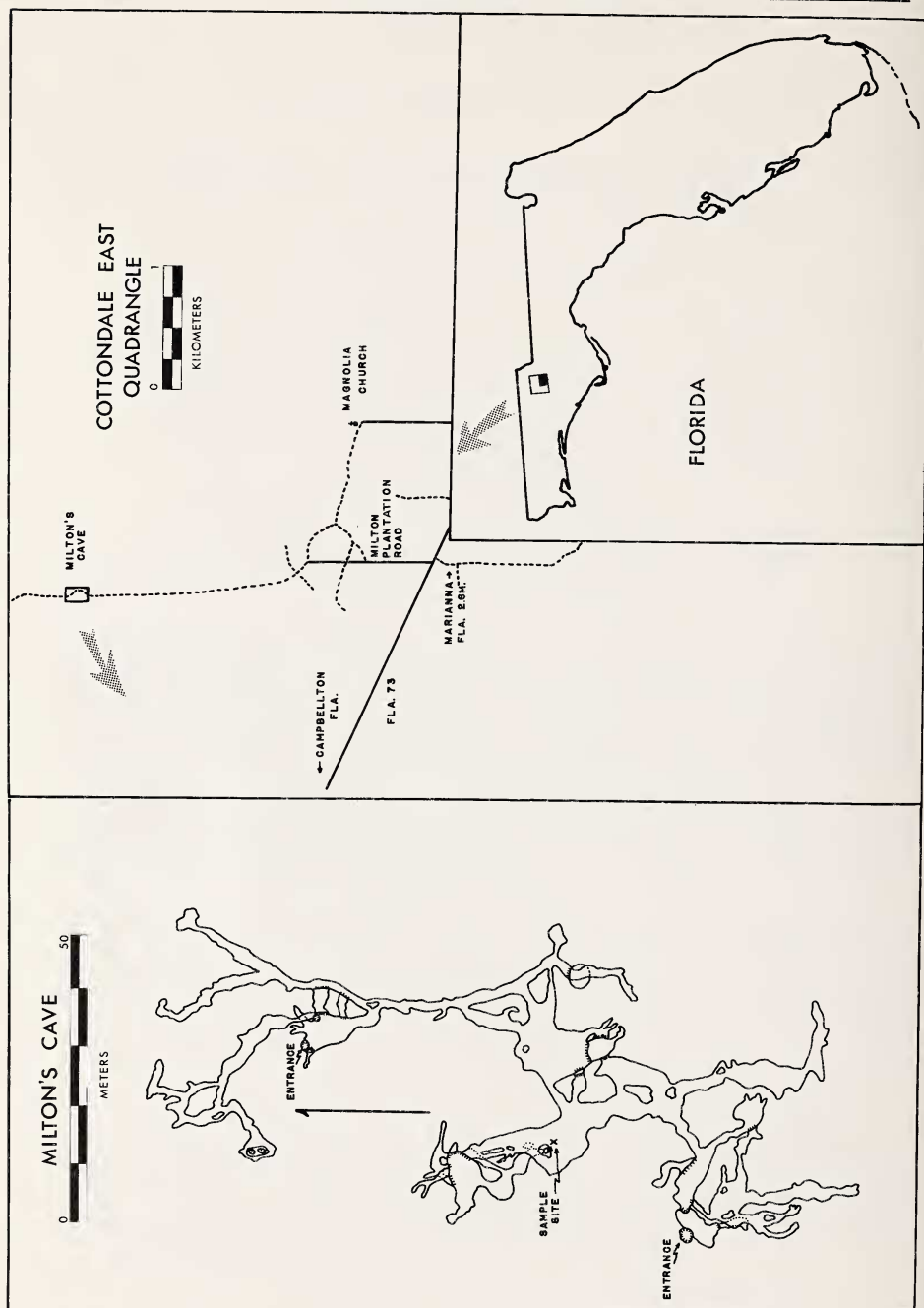


FIGURE 1 Map showing the type locality of *Homo erectus* at Milton's Cave, Florida.

The lutjanid fossils known from North America come from the Miocene of California, *Lutjanus hagari* Jordan and Gilbert, 1919, and the Oligocene of Florida, *Lutjanus avus* Gregory, 1930. The first known fossil of a hoplopagrine snapper (described below) comes from within a few miles of the site of collection of *Lutjanus avus* in northwest Florida (Figure 1). The Hoplopagrinae are otherwise known only by the sole living species, *Hoplopagrus guntheri* Gill (1862a) which ranges from Abrejos (UCLA S-392) and Magdalena (LACM 32086-3) Bays on the west coast of Baja California and Guaymas (CAS IU 7749) in the Gulf of California south to Panama (Walford, 1937). It occurs about reefs from shore to "deep, cold water near the Pearl Islands" (Walford, 1937) in the Gulf of Panama.

Previous authors have compared the hoplopagrines with other lutjanids and with the sparids when searching for the affinities of the subfamily (Gill, 1862a, 1862b; Jordan and Evermann, 1898; Regan, 1913). All agree that the hoplopagrines resemble lutjanids more than sparids, and this seems to be true based on our comparison of the skeletons of most of the North American genera of both families. The new fossil has been compared primarily with North American lutjanids, but osteological resemblances to sparids and pomadasyids have been recorded. References to characters of those families are based on examination of materials listed below. Several old world genera of both families have not been examined, and this should be considered in assessing the comparisons.

MATERIALS AND METHODS

The comparison below of the fossil with recent species of lutjanids, pomadasyids and sparids are based on the following specimens. Neurocranium length was measured from the anterior end of the vomer to the posterior end of the basioccipital. Abbreviations are: California Academy of Sciences (CAS), University of California at Los Angeles (UCLA), and Natural History Museum of Los Angeles County (LACM).

Lutjanidae

Hoplopagrus guntheri Gill: CAS 14158, 460 mm SL, Mexico, Cerralvo Is., 4 March 1945; LACM-VP-F422, Mexico, Gulf of California, Cabo Lobos, 14 Feb. 1970, S. P. Applegate; UCLA S-392, about 410 mm SL, Mexico, Baja California, Abrejos Bay, May, 1954; LACM 31774-1, 208 mm SL, Mexico, Gulf of California, Baja California, just S Pta. Arena, R/V Searcher Sta. 44, 2 Feb. 1971.

Lutjanus apodus (Walbaum): LACM 31732-1, SL unknown (neurocranium 48.9 mm long), Bahamas, San Salvador Island, Graham Harbor, 10 June 1966, E. S. Wing.

Lutjanus campechanus (Poey): LACM 31737-1, 523 mm SL, Florida, Gulf of Mexico, Middle Grounds, Sept. 1969, P. McCaffrey.

Lutjanus griseus (Linnaeus): LACM 31735-1, 393 mm SL, Florida, Monroe Co., Tortugas, 17 or 18 Dec. 1968, C. Combs, H. Austin, H. Matraw;

LACM 31852-1, 460 mm SL, Broward Co., off Hollywood Beach, 18 March 1969, H. Yaffa; LACM 31736-1, 215 mm SL, Florida, Okaloosa Co., mouth Choctawhatchee Bay, 12 Oct. 1968, R. Hastings.

Lutjanus synagris (Linnaeus): LACM 31731-1, ca. 335 mm SL, Florida, Volusia Co., vic. Daytona Beach, summer 1966, M. Gomon.

Ocyurus chrysurus (Bloch): LACM 31853-1, 461 mm SL, Florida, Gulf of Mexico, Middle Grounds. 28° 25' N, 84° 18' W, 10 Nov. 1969, J. Bishop, H. Austin; LACM 31734-1, 245 mm SL, Panama, Atlantic Ocean, San Blas, Holandes Cay, 27 Sept. 1970, J. E. McCosker.

Pristipomoides aquilonaris (Goode and Bean): LACM 31730-1, ca. 110 mm SL, Oregon Station 10892, Gulf of Mexico.

Rhomboplites aurubens (Cuvier): LACM 31738-1, 190 mm SL, Florida, Okaloosa Co., vic. Destin, 2 April 1966, C. Swift; LACM 31733-2, 219 mm SL, and LACM 31733-1, 165 mm SL, Gulf of Mexico, 23 mi SSE of Pensacola, 29 June 1969, S. Bortone.

Pomadasyidae

Anisotremus davidsoni (Steindachner): LACM 32587-1, 319 mm SL, California, Orange Co., Huntington Beach, 8 Aug. 1970, C. Swift, et al.; LACM 32588-1, 298 mm SL, California, Orange Co., Huntington Beach, 5 July 1970, J. Fitch.

Brachydeutereus corvinaeformis Steidachner: LACM 32585-1, neurocranium 38 mm long, Panama, Atlantic, Bahia Limon, 1970, J. E. McCosker.

Haemulon aurolineatum Cuvier: LACM 32584-2, 129 mm SL, Florida, Franklin Co., 15 mi S Alligator Harbor, 10 May 1969, S. Bortone; LACM 31849-6, 151 mm SL, Florida, Gulf of Mexico, Middle Grounds, 12, 13 June 1969, C. Swift and party.

Haemulon plumieri (Lacepede): LACM 32584-1, neurocranium 72 mm long, Florida, Franklin Co., ca. 15 mi S Alligator Harbor, 10 May 1969, S. Bortone; LACM 31849-5, 383 mm SL, Florida, Gulf of Mexico, Middle Grounds, 12, 13 June 1969, C. Swift and party.

Haemulon sciurus (Shaw): LACM 32586-1, neurocranium 52 mm long, Florida, Monroe Co., Vaca Key, June, 1964, K. Ainslie and party.

Orthopristis chrysoptera (Linnaeus): LACM 31848-3, 177 mm SL, LACM 31848-4, 170 mm SL, Florida, Franklin Co., mouth Alligator Harbor, 4 July 1968, C. Swift and party; LACM 32583-1, 188 mm SL, LACM 32583-2, 179 mm SL, Florida, Franklin Co., St. George Island, 11 June 1968, F. W. Vockell.

Sparidae (all from Florida)

Archosargus probatocephalus (Walbaum): LACM 31591-3, 270 mm SL, Okaloosa Co., mouth Choctawhatchee Bay, 11 Sept. 1969, C. Swift and party; LACM 31850-1, SL unknown (neurocranium 32.9 mm long), Santa Rosa Co., Santa Rosa Sound at Gulf Breeze, 15 July 1966, R. W. Hastings.

Calamus nodosus Randall and Caldwell: LACM 31849-2, 242 mm SL,

Gulf of Mexico, Middle Grounds, 28° 30' N, 84° 15' W, 12, 13 June 1969, C. Swift and party.

Calamus arctifrons Goode and Bean: LACM 31537-36, 137 mm SL, and LACM 31537-38, 159 mm SL, Wakulla Co., 5.5 mi WSW St. Marks Light, 6 Sept. 1969, C. Swift and party.

Diplodus holbrooki (Bean): LACM 31848-2, 123 mm SL, Franklin Co., mouth Alligator Harbor, 4 July 1968, C. Swift and party; LACM 31851-1, 159 mm SL, Franklin Co., off mouth Ochlockonee River, 4 Oct. 1969, J. Wiese, R. Lazor.

Lagodon rhomboides (Linnaeus): LACM 31845-1, 143 mm SL, Bay Co., St. Andrews Bay, 14 Oct. 1967, C. Swift and party, LACM 31848-1, 151 mm SL, Franklin Co., mouth Alligator Harbor, 4 July 1968, C. Swift and party.

Pagrus sedecim Ginsburg: LACM 31738-2, head only (neurocranium 51.8 mm long), Okaloosa Co. ca. 15 mi S Destin, 2 April 1966, R. W. Yerger and class; LACM 31849-1, 292 mm SL, Gulf of Mexico, Middle Grounds, 28° 30' N, 84° 15' W, 12, 13 June 1969, C. Swift and party.

Anatomical Abbreviations

The following abbreviations are used in figures 2 to 5:

bo	basioccipital	para	parasphenoid
bs	basisphenoid	pro	prootic
epo	epiotic	pto	pteric
exo	exoccipital	seth	supraethmoid
fr	frontal	soc	supraoccipital
int	intercalar	spho	sphenotic
leth	lateral ethmoid	vo	vomer
pa	parietal		

Hypsocephalus, new genus

Diagnosis: A hoplopagrine lutjanid distinguished from the living and only other known genus of the subfamily, *Hoplopagrus*, by: 1) a skull which is high and deep rather than elongate; 2) supra- and lateral temporal fossae shallow and flattened rather than deeply excavated; 3) a supraoccipital crest extending anterior to a vertical through the center of the bony orbit rather than forward beyond the anterior edge of this orbit; 4) the globular swelling at the posterior end of the parasphenoid excavated posteriorly rather than a solid protuberance; 5) vomerine teeth in a roundish patch rather than a transverse band; 6) molariform palatine teeth present rather than lacking altogether; 7) two rather than one row of teeth for most of the length of the dentary; 8) three rather than two rows of teeth for most of the length of the premaxillary; and 9) a deeply excavated cavity in the basioccipital broadly confluent with the myodome rather than only narrowly excavated and slightly confluent. Type species *Hypsocephalus atlanticus*. The name *Hypsocephalus* (*ψ*os, high or elevated, + cephalus, head) refers to the high, deep skull

and the specific name *atlanticus* refers to the Atlantic Ocean, the general locality of the fossil, in contrast to the eastern Pacific Ocean, the area where the only living relative, *Hoplopagrus*, occurs.

Hypsocephalus atlanticus, new species

Figures 2-7

Holotype: LACM VP 27859, a single neurocranium, 49.4 mm long, with the right posterolateral side broken off, thus the epiotic, exoccipital, pterotic, and intercalar are absent from this side (see below). Other bones found in definite association with, and certainly part of, this one fish are: a left cleithrum about three-fourths complete, the middle half of the right cleithrum, a fragmentary anterior one-third of the right maxillary, the middle two-thirds of the right premaxillary, the anterior one-fifth of the left premaxillary, the middle three-fourths of the right dentary, a small fragment of the antero-dorsal edge of the left dentary, the anterior half of the right articular, the distal two-thirds and the anterior and proximal one-fourth of the right hyomandibular, impressions of three anterior premaxillary teeth, about half of the right exoccipital with the articular facet for the atlas vertebrae intact, one complete neural arch and spine with the dorsal one-fifth of an anterior abdominal vertebrae attached, several fragmentary branchiostegal rays imbedded in a small piece of limestone, one dorsal spine pterygiophore, and the posterolateral corner of the skull also imbedded in a limestone block.

Locality: LAV Loc. 7189 Florida, Jackson Co., T: 5N, R: 11W, Sec. 13, 2.7 airline miles NW of Marianna (Figure 1), collected by Brooks and Suzanne Ellwood and Edward M. Renner on 2 April 1970. The skull was taken from Milton's Cave (Figure 1) in the lower member of the Crystal River formation, the uppermost Eocene formation in this north Florida area. The locality is a small, intricate cave, and the skull and associated bones were found in a solution cavity of the cave 13.2 ± 0.5 meters below the surface of the ground.

Diagnosis: As for the genus.

DESCRIPTION

Vomer: The ventral surface of the vomer is roughly circular and covered with stout bluntly pointed teeth (Figure 4). The anteriormost tooth is longest and largest in diameter. It is flanked posterolaterally on each side by a tooth slightly smaller in diameter, and about half as high. Posterior to these three, and partially between the posterior two, is a cluster of six small teeth. A seventh small tooth was present as evidenced by a small empty socket just posterior to the lateral robust tooth on the right side. Ventrally a low, rounded keel on the vomer is continuous with that on the parasphenoid. Laterally a low rounded ridge extends posterodorsally to, and is continuous with, that of the lateral ethmoid. The vomer bears a broadly rounded bridge middorsally as well, and with the ventral and lateral ones, the vomer is diamond shaped in cross section just above the tooth patch. Posterodorsally the dorsal ridge

bifurcates narrowly around the narrow rostral fenestra (of Starks, 1926) to meet the supraethmoid.

Comparison: In *Hoplopagrus* the vomerine tooth patch is narrow antero-posteriorly and wider laterally; an anterior transverse row of three or four stout, almost molariform teeth is followed by a row of four to six much smaller teeth similarly proportioned. All the living snapper genera known have villiform vomerine teeth (when they are present), and the vomerine tooth patch assumes a variety of shapes (Gill, 1884; Regan, 1913; Norman, 1966; Anderson, 1967).

Parasphenoid: The anterior half of the parasphenoid bears a wide, thin ventral keel, which is least developed anteriorly at the vomer-parasphenoid articulation (Figure 2). The keel extends further ventrally to the posterior and abruptly ends in 90° angle ventral to the ascending parasphenoid processes articulating with the prootics. Just posterior to the keel, the parasphenoid expands into a globular swelling that is concave posteriorly, and the parasphenoid continues posteriorly as a narrow, dorsoventrally flattened flange ventral to, and articulating dorsally with the basioccipital.

Comparison: The parasphenoid of *Hoplopagrus* is similar to *Hypsocephalus* except that the swollen brace for the upper pharyngeals is not as strongly developed. The parasphenoid of *Lutjanus* lacks this swelling, is relatively longer, and is keeled ventrally. In *Ocyurus* a strong, rounded ridge extends laterally and posterodorsally from the posterior end of the parasphenoid along the ventral and anterolateral edge of each otic bulla. In *Ocyurus* the keel on the parasphenoid is very low. In all of the above except *Ocyurus* the parasphenoid is straight, and the ventral edges of the vomerine tooth patch, of the parasphenoid keel, and of the basioccipital lie along a straight line. The ventral surface of the anterior half of the parasphenoid is slightly concave in *Pristipomoides* and *Rhomboplites*. In *Rhomboplites*, *Pristipomoides*, and *Ocyurus* the longitudinal profile of the parasphenoid is a shallow V. The ventralmost point is at the posterior end of the keel, just ventral to the ascending processes.

Lateral Ethmoid: The lateral ethmoid is essentially rectangular antero-posteriorly. The ventral edge broadly articulates with the parasphenoid, and its anteroventral and posteroventral angles bear short robust pillars which articulate with the palatine. The posterior pillar is shorter and its flat, longitudinally oval facet faces ventrally. The flat oval surface of the anterior pillar faces about equally anteriorly, laterally, and dorsally. The anterior pillar lies on a ridge extending from the lateral corner of the vomer, through the facet, and posterodorsally to the posteromedial portion of the lateral ethmoid where it converges with a thick vertical ridge on the posterior edge of the lateral ethmoid. This vertical ridge narrows ventrally, terminating in the posterior facet. Dorsally it thickens, extends laterally, and its cancellous dorsal surface articulates with the lateral edge of the frontal. A space separates the two lateral ethmoids medially just under the frontals. The lateral ethmoids meet

along the middle one-fourth of the vertical distance between the frontals and the parasphenoid. Ventral to this midline contact the lateral ethmoids are separated narrowly to their ventral articulation with the parasphenoid. Ventral to and slightly lateral to the anterior opening of the supraorbital lateral line canal in the frontal, the olfactory canal courses anteriorly from

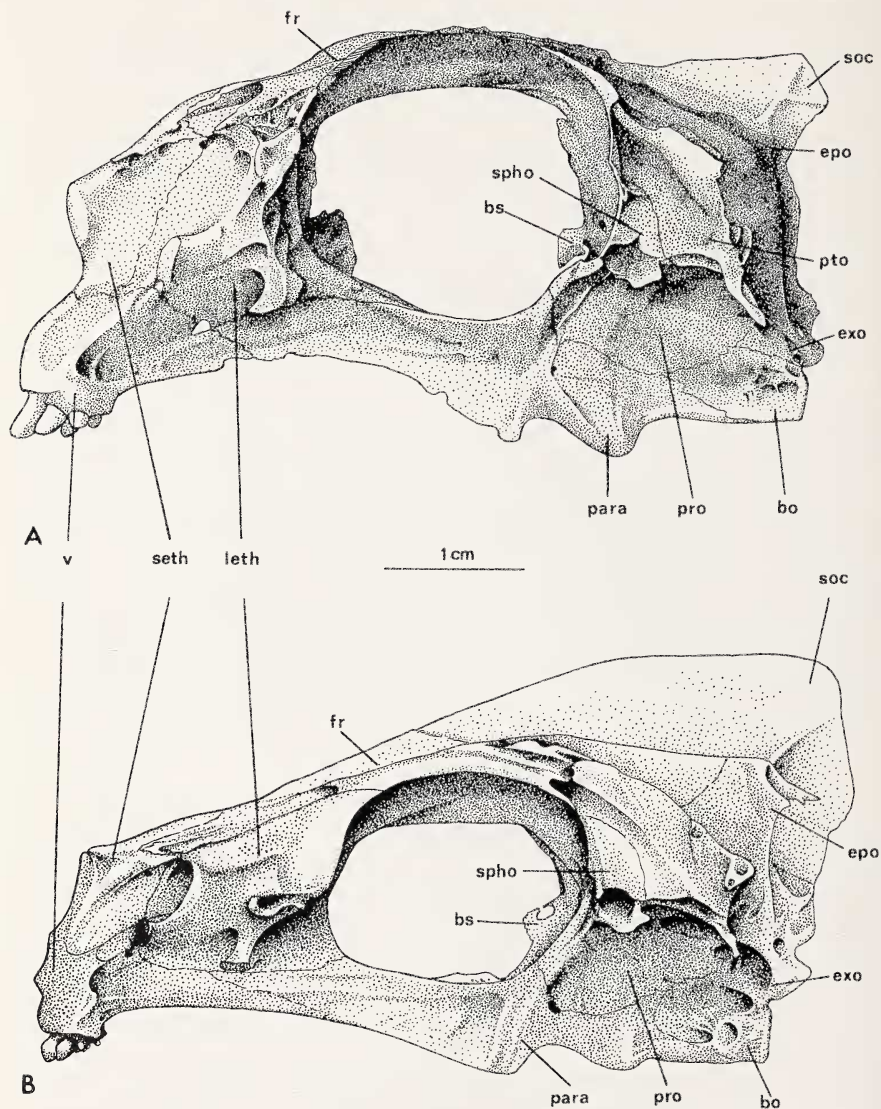


FIGURE 2. Lateral view of the neurocrania. A, *Hypsocephalus atlanticus* (LACMVP 27859); B, *Hoplopagrus guntheri* (LACM 31774-1).

the orbital cavity through the lateral ethmoid. This canal is a vertical oval in cross section, 3 mm high and 1 mm wide.

Comparison: The two facets for articulation with the palatine are similar to *Hypsocephalus* in *Hoplopagrus*, but in the latter both face slightly more laterally. In *Ocyurus* and *Lutjanus* the anterior facet faces anteroventrally and slightly laterally, and the posterior one faces ventrally and slightly anteriorly. The facets are at the ends of ridgelike struts of bone in the above genera. *Rhomboplites* and *Pristipomoides* bear these two facets in the same orientation as in *Hypsocephalus*, but they are only slightly raised from the lateral bone surface. The third facet which receives the medial side of the lachrymal lies slightly more dorsal than the anterior palatine facet and is dorsal, lateral and slightly posterior to the posterior palatine facet in *Hypsocephalus*, *Hoplopagrus*, *Ocyurus*, and *Lutjanus*. In *Rhomboplites* and *Pristipomoides* the lachrymal facet is on the same level as the anterior palatine facet, and is above and lateral to the posterior one. *Hoplopagrus* shares with *Hypsocephalus* the strongly developed dorsal and dorsolateral portion of the lateral ethmoids. In *Lutjanus*, *Ocyurus*, and *Pristipomoides*, this surface faces laterally and slightly anteriorly, meeting about perpendicularly with the lateral edge of the frontals. In *Rhomboplites* the lateral ethmoid faces more dorsally than in *Lutjanus* and *Ocyurus*, but still meets the frontal with an abrupt angle rather than through a continuous surface as in the hoplopagrines. The olfactory nerve foramen is large in *Hoplopagrus* (which has an exceptionally large nasal capsule) and about the same relative size as in *Hypsocephalus* in the remaining recent genera.

Supraethmoid: The dorsal surface of the supraethmoid is shaped like a posteriorly directed arrowhead, its posterolateral surfaces bounded by the frontals (Figure 3). The supraethmoid is widest just anterior to the frontals; immediately anterior to this widest point it narrows in width by about one-third. Here the anterolateral transverse edges each bear a short pointed process. A thick median ridge extends anteriorly a short distance and then bends perpendicularly and continues ventrally. The ridge narrows ventrally and the anterior edge flattens out anteroventrally around the rostral fenestra. This thick anterodorsal ridge of the supraethmoid narrows slightly posteroventrally before the lateral surfaces of the bone flare laterally to meet the lateral ethmoids.

Comparison: The dorsal surface of the supraethmoid is similar to *Hypsocephalus* in *Pristipomoides* and is reduced to a small square in *Rhomboplites* and *Ocyurus*. In *Hoplopagrus* it is oblong, gently rounded anteriorly and directed posteriorly between the frontals. It is long and slender in *Lutjanus*, where it is widest between the anterior tips of the frontals and gradually narrows posteriorly. In the recent genera the anterior end of the dorsal surface of the supraethmoid meets at right angles with the vertical, mid-longitudinal ridge of the anterior surface which slopes ventrally and anteriorly. The rostral fenestra is large in *Hoplopagrus* and *Pristipomoides* (as in *Hypsocephalus*),

small in *Ocyurus* and *L. synagris*, and absent in *Rhomboplites*, *L. campechanus*, and *L. griseus*. In *Hoplopagrus* a low ridge is present parallel and lateral to the median ridge. It is absent in *Hypsocephalus* and is absent or only present as a slight suggestion of a raised area in the other recent genera.

Frontal: The frontals are thin and dip medially to produce a shallowly concave interorbital region. The articulation between them extends posteriorly and slightly dorsally from the posterior apex of the supraethmoid to a vertical through the middle of the bony orbit and the beginning of the supraoccipital crest. Each frontal continues posteriorly and laterally of the supraoccipital crest to a vertical between the two facets for articulation of the hyomandibular. Anteriorly, laterally, and ventrally the frontals firmly articulate with the lateral ethmoids, and continue posteriorly to rim the orbit. Along the posterodorsal edge of each orbit they meet the sphenotics, the articulation itself continues

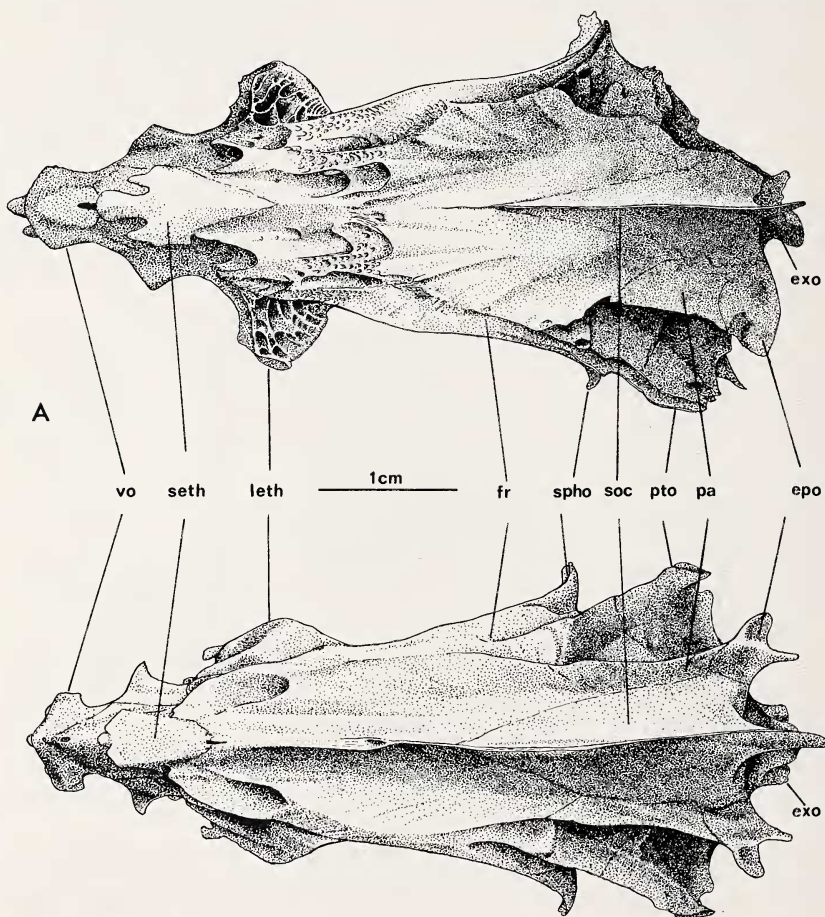


FIGURE 3. Dorsal view of the neurocrania. A, *Hypsocephalus atlanticus* (LACMVP 27859); B, *Hoplopagrus guntheri* (LACM 31774-1).

medially and posteromedially of the dorsal edge of the orbit as a shelf forming the anterolateral edge of the supratemporal fossae. This shelf continues posteriorly and laterally on the pterotic bone.

Comparison: In all the recent lutjanid genera examined except *Pristipomoides* the frontals contribute to the anterior portion of the supraoccipital crest, slightly in *Rhomboplites* and considerably in the remaining genera. In *Pristipomoides* and *Lutjanus apodus* the crest extends anterior to reach the posterior third of the orbit. In *Rhomboplites* and *Lutjanus griseus* the crest reaches only to a vertical line through the anterior third of the orbit diameter. The longitudinal ridge which extends ventrally to meet the pterospheonoid from the medial portion of each frontal is short in *Rhomboplites* and *Ocyurus*. This ridge extends more ventrally in *Hoplopagrus* and *Lutjanus* to form about the dorsal third of the wall separating the braincase from the orbit. The anterior supraorbital canal foramen in the frontal opens over the anterior third of the orbit in *Rhomboplites* and *Lutjanus griseus*, dorsal and slightly medial to the anterior edge of the orbit in *L. synagris* and *L. apodus*, and slightly anterior to the front edge of the orbit in *Pristipomoides*, *Ocyurus*, *Hoplopagrus*, and *Hypsocephalus*.

Parietal: Each parietal is largely a flat shelf which extends laterally and slightly dorsally from near the posterodorsal margin of the orbit to the epiotic posteriorly. The shelf forms the ventral and lateral surface of the shallow supratemporal fossa. From the lateral edge of this shelf, the parietal extends ventrally toward the pterotic about as far as it does medially toward the supraoccipital. The vertical, laterally facing portion forms (with the frontal anteriorly and the epiotic posteriorly) the medial boundary of the lateral temporal fossa. This ridge diverges laterally toward the posterior region of the skull. Dorsally the parietal bears a shallow longitudinal trough.

Comparison: Only the parietal of *Rhomboplites* resembles that of *Hypsocephalus*, largely covering the floor of the supratemporal fossae and extending laterally and slightly dorsally into the low ridges extending from the epiotics to the frontals. In *Hoplopagrus*, *Ocyurus*, and *Lutjanus* these ridges resemble each other and are oriented vertically and slightly laterally. In *Pristipomoides* this ridge is largely restricted to the parietal bone, with a slight contribution from the frontals anteriorly and no involvement of the epiotics posteriorly. The ridges are parallel to the supraoccipital crest in *Rhomboplites*, *Ocyurus*, *Lutjanus griseus*, *L. synagris*, and *L. campechanus*. They diverge slightly laterally to the posterior in *Hoplopagrus*, *Pristipomoides*, and *L. apodus*.

Epiotic: The dorsal surface of the epiotics inclines slightly posteriorly and slightly laterally. The lateral half of the dorsal surface is shallowly excavated for articulation with the dorsal limb of the posttemporal. The medial half of the dorsal surface is slightly depressed, and there is no trace of a posteriorly directed spine. The epiotic articulates ventrally with the exoccipital via a strong columnar strut directed ventrally and slightly medially

and posteriorly. This strut along with that of the exoccipital, forms the posterolateral corner of the temporal region.

Comparison: Just ventromedial to the epiotic facet for receiving the upper limb of the posttemporal, *Hoplopagrus*, *Ocyurus*, *Rhomboplites*, and *Lutjanus* bear a posteriorly directed process. This spine is lacking in *Hypsocephalus* and *Pristipomoides*. The facet for the posttemporal faces posteriorly and dorsolaterally in *Ocyurus*, *Hoplopagrus*, and *Lutjanus* and almost directly dorsally in *Rhomboplites* and *Pristipomoides*.

Prootic: The prootic is gently inflated laterally and dorsally to accommodate the anterior end of the otolith. Posteriorly the prootic articulates with the basioccipital below and the exoccipital above. It joins broadly with the parasphenoid ventrally. A narrow portion directed dorsally and slightly laterally occupies the ventral half of the anterior hyomandibular facet and articulates with the sphenotic dorsally. A short shelf extends laterally from and borders the posteroventral aspect of this facet. Medially the prootics meet as a flat shelf forming the floor of the anterior one-third of the brain-case and abut against the basisphenoid anteriorly. Each posterior and vertical edge of this shelf extends anterolaterally from the anterior end of a thin medial process of the basioccipital to form the anteromedial wall of the chamber for the saccular otolith. Anteriorly and dorsally the prootic forms a transverse squarish plate articulating with the basisphenoid ventromedially, the pterosphenoid dorsomedially, and the sphenotic dorsally. Just dorsolateral to the tripartite juncture with the basisphenoid and pterosphenoid the prootic bears a large foramen. The pars jugularis, with its two large foramina, is overlain by a narrow arch which extends ventrally, anteriorly, and medially from the anteroventral corner of the anterior hyomandibular facet, and broadly inserts on the anterolateral edge of the prootic. The shelf bordering the posteroventral edge of the anterior hyomandibular facet bears a thin blade which extends ventrally parallel and posterolateral to this arch. This blade terminates in a free end about half way along the arch. The prootic bears another free ending blade which originates on the medial side of the anterolateral edge of the prootic. It extends dorsally, parallel, and anteromedial to this arch.

Comparison: The arch over the pars jugularis consists of a single pillar of bone in *Rhomboplites*, *Pristipomoides*, *Ocyurus*, and *Lutjanus*. In *Hoplopagrus* the two incomplete arches parallel to the main one (as in *Hypsocephalus*) are present but not as extensively developed. In *Hoplopagrus* the pars jugularis is partly bridged over anteriorly by three narrow flat shelves of bone: a ventrolateral projection of the pterosphenoid, a ventromedial extension of the sphenotic and a medial extension from the prootic where it abuts the pterotic anterior to the hyomandibular facet. This arrangement is only present in large *Hoplopagrus*. The posteroventral portion of the prootic is inflated to accommodate the large otolith in *Rhomboplites*, *Ocyurus*, *Pristipomoides*, *Lutjanus synagris*, and *L. campechanus*. In *L. griseus*

and *L. apodus* it is only slightly expanded, but more so than in *Hoplopagrus* which has a small otolith, as apparently did *Hypsocephalus*.

Sphenotic: The sphenotic is a flat bone which occupies the middle one-third of the posterior face of the orbit and the dorsal one-half of the anterior hyomandibular facet (Figure 2). The large eye and foreshortened skull leave the sphenotic (and pterotic) with greatest dimensions in a vertical rather than longitudinal direction. The sphenotic articulates with the pterotic posteriorly via a suture proceeding vertically and then anteriorly from the posterior margin of the anterior hyomandibular facet. The sphenotic articulates with the prootic ventrally via the anterior hyomandibular facet and via an articulation extending medially from this facet to the articulation with the ptersphenoid. Dorsally the sphenotic articulates with the frontal.

Comparison: In *Lutjanus griseus*, *L. campechanus*, *Ocyurus*, and *Rhomboplites* the sphenotic lies more dorsal and more anterior in the posterodorsal quarter of the orbit. In *Lutjanus synagris*, *L. apodus*, *Pristipomoides*, and *Hoplopagrus* it is placed only slightly more dorsal than in *Hypsocephalus*. In all of the recent lutjanid genera examined the sphenotic bears a laterally directed spine which originates on the posterior surface at the anterodorsal corner of the anterior hyomandibular facet. This region is broken on both sides in *Hypsocephalus*.

Pterotic: Like the sphenotic, the pterotic is oriented largely vertically. Its dorsal two-thirds directly posterior to the sphenotic, and the ventral one-third is posterior to as well as slightly ventral to the anterior hyomandibular facet. The pterotic bears the entire posterior hyomandibular facet. This facet is horizontally elongate, and slightly wider posteriorly. It lies directly posterior to the anterior facet, from which it is slightly separated. The short pointed process of the pterotic just below and lateral to the articular surface for the ventral limb of the posttemporal (on the intercalar) is directed ventrally and only slightly laterally and posteriorly. Just ventral and medial to the posterior hyomandibular facet, a shelf of the pterotic extends medially and slightly ventrally to articulate with the intercalar and exoccipital posteriorly, and the prootic anteriorly. The pterotic occupies the posterolateral edge of the skull and has a ridge which bears the temporal lateral line canal. From this ridge the pterotic dips ventromedially to meet (anterior to posterior) the frontal, parietal, epiotic, and exoccipital, and forms the lateral border and floor of the lateral temporal fossa.

Comparison: The pterotic in *Rhomboplites*, *Ocyurus*, *Pristipomoides*, and *Lutjanus* extends almost directly posterior from the dorsal half of the orbit. In these genera the process on the posterior lateral border of pterotic extends largely posteriorly and only slightly laterally and ventrally. In *Hoplopagrus* this spine projects much more ventrally as it does in *Hypsocephalus*, and the pterotic is posterior to the middle half of the orbit in both of these genera as well.

Intercalar: The intercalar is flat and occupies an almost horizontal, ven-

trally facing surface (Figure 4). It is narrowly pointed laterally just ventral and posterior to the posterolateral spine of the pterotic. The intercalar rapidly widens medially and slightly ventrally to articulate broadly with the prootic anteriorly and exoccipital posteriorly. This articulation lies just dorsolateral to a shallow longitudinal groove marking the dorsal edge of the otic bulla. The transversely oval, concave facet which receives the lower limb of the posttemporal faces directly posterior and about three-fourths of the facet lies above the spine of the pterotic just lateral to the facet.

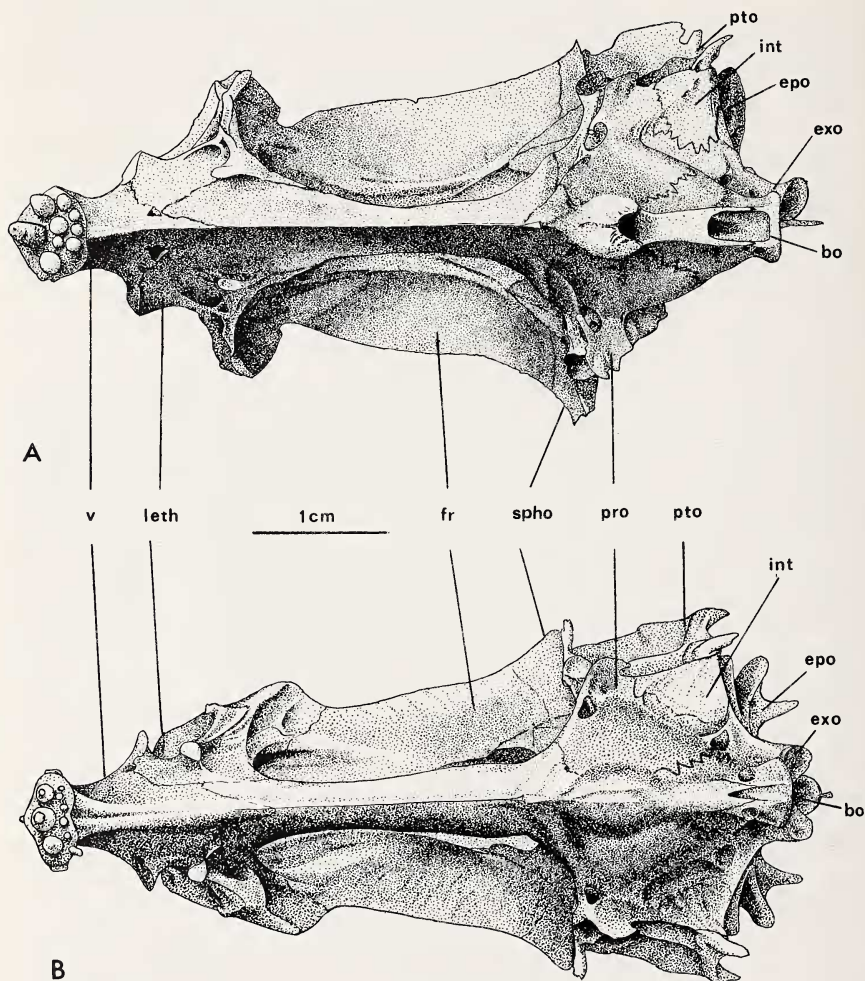


FIGURE 4. Ventral view of the neurocrania. A, *Hypsocephalus atlanticus* (LACMPV 27859); B, *Hoplopagrus guntheri* (LACM 31774-1).

Comparison: The intercalar is roughly trapezoidal in *Lutjanus*, *Ocyurus*, and *Rhomboplites*, the anterior and posterior edges roughly paralleling each other, and the medial and lateral ones converging anteriorly. The intercalar is quite similar in orientation and shape in *Hypsocephalus* and *Hoplopagrus*. The facet for reception of the posttemporal lies entirely above the lateral pterotic process in *Hoplopagrus*. In the other genera examined the facet lies directly medial to the process, and the facet is directed laterally as well as posteriorly rather than just to the posterior. The facet is immediately medial to the process of the pterotic in *Lutjanus*, *Hoplopagrus*, and *Hypsocephalus*, but is separated by a short, thin, horizontal ridge in *Rhomboplites* and *Ocyurus*. In *Pristipomoides* the facet is posterior as well as medial to, and widely separated from the pterotic process.

Basisphenoid: Only the dorsal half of the basisphenoid is present, assuming the ventral, basal portion was originally possessed. A thin, compressed piece of this basal limb extends anteroventrally. Posterodorsally it is narrowly confluent with the two, dorsolaterally extending wings. From this attachment these two wings spread a short distance, transversely and fanlike, to form a small part of the central anteroventral wall of the braincase. They articulate broadly with the pterosphenoids laterally. Just posterior to the basisphenoid is the large hypophyseal foramen which the ventral and posteroventral tips of each fan virtually encircle before articulating with the two prootics posteriorly. The dorsal tips of the basisphenoid rise only slightly to articulate with the pterosphenoids, and form the ventral border of a large, vertically elongate opening which extends dorsally to the underside of the frontals and lies between the brain and orbital region.

Comparison: The dorsal edge of the basisphenoid in *Hoplopagrus*, as in *Hypsocephalus*, curves dorsally only slightly towards the pterosphenoids. In *Lutjanus*, *Ocyurus*, *Pristipomoides*, and *Rhomboplites* the dorsolateral edges of the basisphenoid curve dorsally, entering the ventrolateral as well as the ventral edge of the cavity connecting brain and orbit. The hypophyseal foramen is larger (*Lutjanus apodus*), about the same size (*Pristipomoides*, *Rhomboplites*), or smaller (*Ocyurus*, *Hoplopagrus*, *Lutjanus synagris*, *L. campecharus*, *L. griseus*) than in *Hypsocephalus*. The foramen is rounded in *Hypsocephalus* and *Hoplopagrus*, and is transversely oval in the other snapper genera.

A slight projection extends anterodorsally into the orbit from the basal portion of the basisphenoid in *Hoplopagrus*. There is no such projection on the basal portion in *Rhomboplites* and *Pristipomoides*, but a broad flat projection is present in *Lutjanus* and *Ocyurus*.

Pterosphenoid: The two pterosphenoids form much of the anterior wall of the braincase and, much of the lateral border of the large foramen connecting the braincase with the orbital region. About the middle of the medial margin of each bears a short, medially directed point of bone. On the left side a small foramen occurs ventral and slightly lateral to this projection, and

another foramen is present dorsolaterally about half way between the tip of the projection and the surface of articulation with the frontal. On the right side the corresponding ventrolateral foramen is lacking, and in the position of the dorsolateral one are two smaller foramina. The pterospheonoid articulates, in a broad arc laterally (dorsal to ventral) with the frontal, sphenotic, prootic, and basisphenoid, respectively.

Comparison: In *Lutjanus*, *Rhomboplites*, and *Ocyurus* the pterospheonoid occupies about the same relative position as in *Hypsocephalus*, and bears slight (*Lutjanus*, *Rhomboplites*) to prominent, narrowly pointed medial projections (*Ocyurus*). The pterospheonoids are straight edged medially in *Hoplopagrus*, and lack any medial projections. The pterospheonoids are less extensive in *Hoplopagrus*, where the frontals extend ventrally to occupy the dorsolateral walls of the cavity connecting the brain with the orbit. This cavity is a wide vertical oval in *Hypsocephalus*, only slightly elongated dorsoventrally in *Hoplopagrus*, much elongated dorsoventrally in *Lutjanus* and *Ocyurus*, and narrowly constricted in *Rhomboplites* with a roughly circular opening dorsal and ventral to a narrow interspace. In *Pristipomoides* the pterospheonoids firmly articulate medially for the middle third of the vertical distance between the dorsal edge of the basisphenoid and the underside of the frontals. Thus the orbit and brain cavity are connected by two subequal circular openings occupying the dorsal and ventral one-third of this distance.

Basioccipital: The posterior basioccipital facet is vertical, facing directly posterior. Anterior to this facet the bone is almost a vertical rectangle in cross section, compressed to about two-thirds the facet width. Ventrally it is deeply excavated and this cavitation extends anteriorly above the transverse posterior end of the parasphenoid. Further dorsally and anteriorly this cavity opens widely into the posterior myodome. Laterally the basioccipital forms the ventrolateral wall of the posterior portion of the chamber for the saccular otolith. A thin, compressed, medial extension runs anteriorly and slightly dorsally to articulate with the thick median juncture of the prootics.

Comparison: The whole posterior facet of the basioccipital lies in one plane and faces somewhat posterodorsally in *Lutjanus*, *Ocyurus*, and *Rhomboplites*. The posterior facet faces posteriorly in *Hoplopagrus*. The anterodorsal portions which enter the otic bulla are somewhat more expanded in *Lutjanus synagris* and *Ocyurus*, but are compressed in *Lutjanus griseus* and *Hoplopagrus*. *Rhomboplites* and *Pristipomoides* have large otoliths and a widely expanded basioccipital. The basioccipital is only narrowly excavated ventrally in *Lutjanus* and the cavity is not confluent with the posterior myodome. The cavity is small and narrowly confluent in *Hoplopagrus*, and large and confluent in *Ocyurus*, *Pristipomoides*, and *Rhomboplites*. In *Rhomboplites* the basioccipital is wider (almost square) just anterior to the posterior facet rather than being narrowly compressed and rectangular.

Supraoccipital: The supraoccipital penetrates anteriorly between the frontals to a position slightly behind a vertical through the middle of the

orbit. It widens posteriorly and along the posterior edge of the skull occupies the medial half of each supratemporal fossa. The lateral surfaces slope slightly ventrolaterally to the parietal and epiotic. The supraoccipital crest is broken dorsally and is described from photographs taken before it was collected when the crest was more complete. The supraoccipital crest is low, only slightly higher than the dorsal surface of the skull anteriorly. A slight ridge extends posterodorsally from the posterodorsal border of the skull on each side of the crest. About 5 mm along this ridge, another ridge extends from it posteriorly and slightly ventrally.

Comparison: The supraoccipital (in the supraoccipital crest) extends anteriorly to a vertical through the center of the orbit in *Hoplopagrus*, *Rhomboplites*, and *Ocyurus*. In *Lutjanus* and *Pristipomoides* it extends only to a vertical through the posterior one quarter of the horizontal orbit diameter. The ridge extending posterodorsally from the posterodorsal corner of the skull bears a ventral branch distally in *Hoplopagrus*, *Rhomboplites*, and *Ocyurus*, but the ventral branch is lacking in *Lutjanus*. In *Rhomboplites*, *Ocyurus*, and *Hypsocephalus* the main branch extends to the posterodorsal apex of the supraoccipital crest, but in *Lutjanus* and *Pristipomoides* this ridge reaches to a point a little below the apex along the vertical posterior edge of the crest.

Exoccipital: Although the right exoccipital is fragmentary, the left is complete. Clearly both met in the midline over the basioccipital, and the ventral, lateral and at least dorsolateral walls of the foramen magnum were bounded by the exoccipitals (Figure 5). Each flat facet receiving the dorsal portion of the atlas vertebra is a regular transverse oval facing ventromedially. The medial edge terminates a millimeter or two short of the midline and the exoccipital facets did not form a continuous articular surface. From the facet a strong pillar of bone extends anterodorsolaterally and forms the posterolateral corner

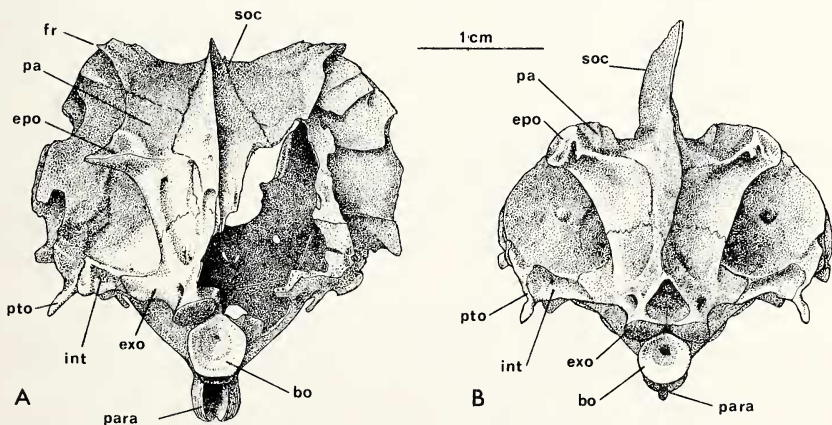


FIGURE 5. Posterior view of the neurocrania. A, *Hypsocephalus atlanticus* (LACMVP 27859); B, *Hoplopagrus guntheri* (LACM 31774-1).

of the skull. The ridges soon bifurcate, one branch extending dorsally and slightly anteriorly to the epiotic, and the other laterally and slightly anterior to the intercalar and pterotic. A foramen is present just dorsolateral to the articular facet for the atlas vertebra, and another larger one pierces the exoccipital just anterior to the pillar of bone which extends laterally towards the pterotic.

Comparison: Medial extensions from, and about half as wide as, the exoccipital facets form a continuous articular surface across the midline in *Ocyurus*, *Rhomboplites*, *Pristipomoides*, and *Lutjanus*. These facets have narrowed medial extensions in *Hoplopagrus* but do not meet in the midline. The exoccipitals have greater antero-posterior extent in *Lutjanus* and *Ocyurus* than in *Rhomboplites*, *Hoplopagrus*, and *Hypsocephalus*.

Dentary: About three-fourths of the right dentary is present, and its medial side is covered with limestone (Figure 6). Only about one-eighth of the left dentary remains. The dentary is robust and bears a lateral row of robust, bluntly pointed teeth about the size of the larger vomerine teeth. These lateral teeth diminish slightly in size posteriorly. An inner row of robust teeth about half the size of the outer teeth is visible on the fragmentary left dentary. This inner row extends backward to at least half the length of the dorsal limb of the dentary. The symphysis is lacking, but the dentaries seem to be oriented as they were in life, and appear to have met via a deep, strong articulation. The dentary rises sharply posteriorly and it appears that the length of the intact dentary is subequal to the vertical distance between the posterior ends.

Comparison: *Hypsocephalus* and *Hoplopagrus* have an outer row of bluntly pointed robust teeth. In *Hypsocephalus* the nature of the dentition on the anterior ends of the dentaries is unknown. In *Hoplopagrus* two or three larger blunt canines are developed anteriorly in each dentary, and the inner row is restricted to two or three smaller teeth present just behind these canines. In the remaining genera a single row of slender to robust canines is followed by a small number of fine inner teeth restricted to the anterior one-third or less of each dentary.

Articular: Only the anterior one-third of the right articular is present, and it essentially occupies its normal position between the posterior limbs of the dentary (Figure 6). The articular is deep and robust like the dentary.

Comparison: The most that can be seen from the fragmentary articular is that it is relatively deep, at least anteriorly, as are the articulars in the other genera.

Cleithrum: Only a fragment of the left cleithrum is present (Figure 6). More complete and relatively intact cleithra were present in the cave before the skull was collected, and they are described from photographs of two views. Three-fourths of the left cleithrum and the middle third of the right one were present. The upper limb was pointed on the anterodorsal edge. A short distance below it widens perpendicularly backward, so the flat plate of the dorsal limb has a largely horizontal dorsal surface. The posterior edge was about

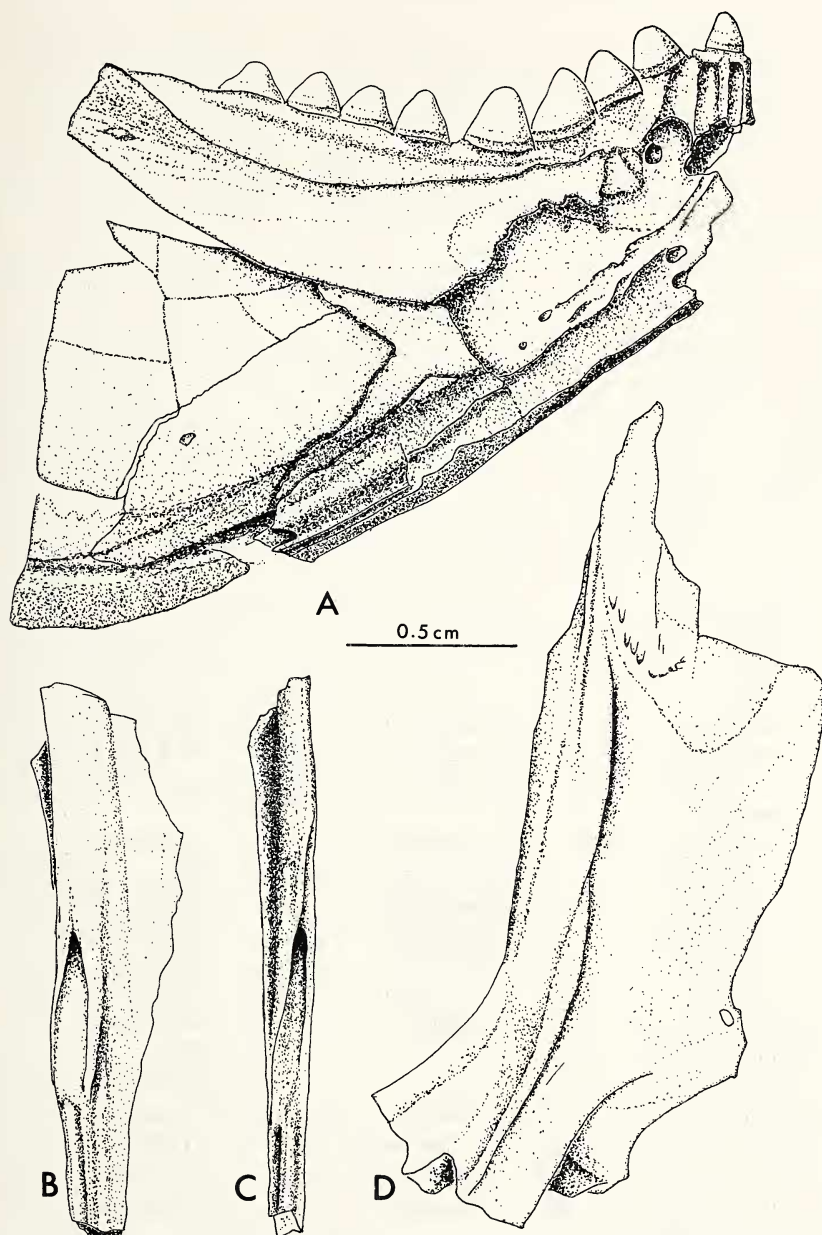


FIGURE 6. Bones of *Hypsocephalus atlanticus*. A, Lateral view of right dentary and anterior portion of the right articular. B, Lateral view of distal two-thirds of the right hyomandibular. C, Posterior view of B. D, Lateral and slightly anterior view of the fragmentary left cleithrum.

vertical and the dorsal limb is roughly uniform in width below the narrow anterodorsal point. The posteroventral angle of the dorsal limb bears a short, rounded, flat projection just above the position of the coracoid. The anteroventral limb possesses a wide flange laterally. Both ventral limb flanges lack the anterior one-fourth of their extent. A shallow groove is present on the lateral edge and it extends dorsally and anteroventrally about one-half the distance of each limb. The dorsal and posterior edge of the upper limb are broken so the exact shape is not known.

Comparison: The cleithra of recent genera show only minor differences which are not discernible on the fossil.

Hyomandibular: Most of the ventral limb and the anterior third of the proximal articular portion of the right hyomandibular are present. Only the anterior facet which articulates with the skull is present of the three proximal articular surfaces of the hyomandibular. The facet is flat, slightly oval dorsoventrally, and bears a small notch ventrally. From this facet a ridge extends posteriorly and laterally. It runs into a strong, dorsoventral ridge which is directed anterolaterally, and is broken dorsally and ventrally. The anterior flat blade of the hyomandibular extends ventrally a short distance to a transverse break in the bone. The medial ridge leading from the anterior to the posterior articular facet is broken just behind the anterior facet. The thickened posterior edge of the hyomandibular is longitudinally oval in cross section, and is hollow in the distal one-third. The proximal two-thirds is hollow also, and opens out posterolaterally via an elongate oval foramen. Along the posterior edge of the shaft a groove originates near the distal end of this foramen. The groove widens and deepens proximally to the broken end which lies about two-thirds of the estimated total length of the intact bone from the distal end (Figure 6).

Maxillary: Only the ventral half of the anterior third of the maxillary is present (Figure 7 C, D, H). The anterior excavation which accommodates the premaxillary was high and narrow. The ventral edge of the medial side bears a low rounded swelling which articulates laterally with the ascending process of the premaxillary. Dorsal to this swelling extends a low, rounded, vertical ridge, which is about as long as the thickness of the shaft of the maxillary. The shelf extending anterolaterally from the head of the maxillary was thin and does not appear to have been expanded distally.

Comparison: The medial articular surface and ridge dorsal to it are relatively smaller in the fossil than in *Hoplopagrus*. The ridge is sharp rather than rounded in *Hoplopagrus* as well. The ridge is rather sharp edged and much higher and longer in all the other recent snapper genera. The ridge is straight edged in the hoplopagrines and *Rhomboplites* and is a raised semicircle in the other recent genera.

Premaxillary: The premaxillary is dorsoventrally flattened and bears an outer row of enlarged teeth about the same size as those on the dentary and an inner double row of molariform teeth about one-third the size of the outer

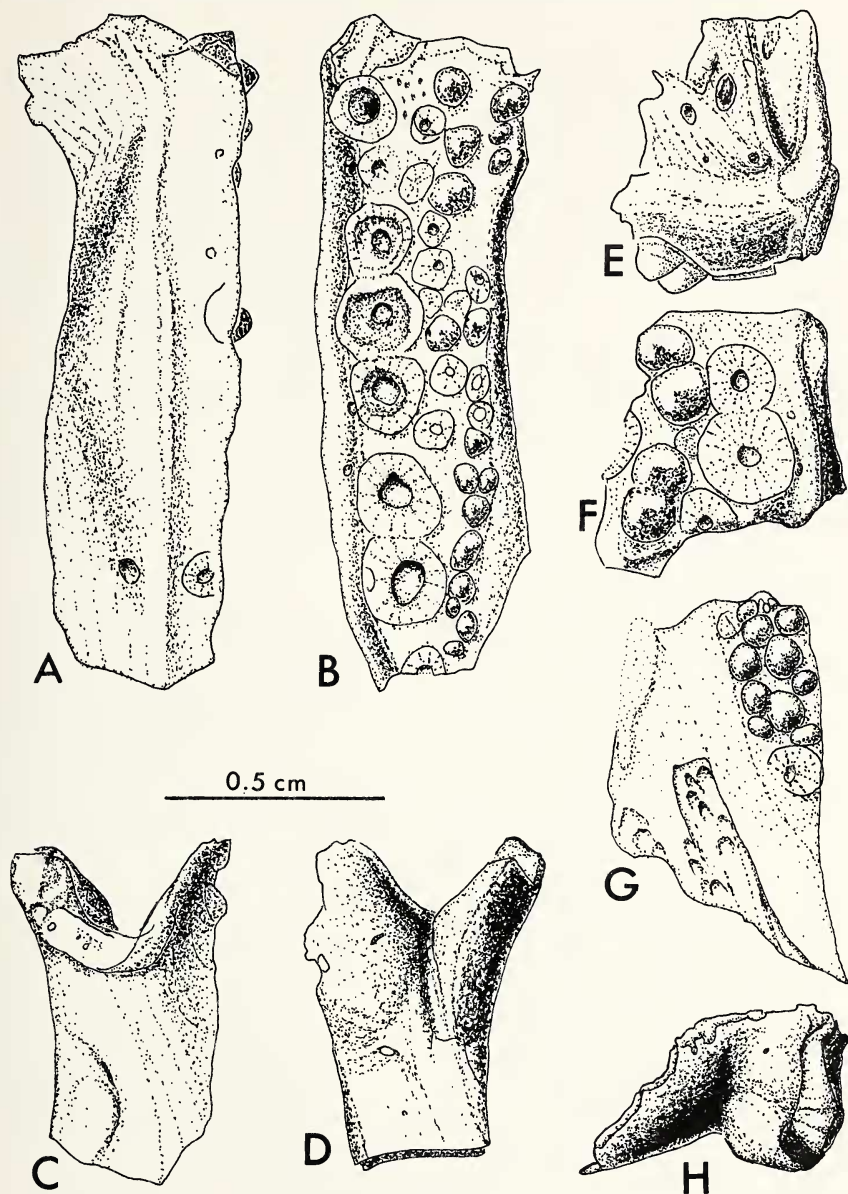


FIGURE 7. Bones of the jaws and palate of *Hypsocephalus atlanticus*. A, Anterior view of anterior two-thirds of right premaxillary. B, Ventral view of A. C, Dorsal view of the head of the right maxillary. D, Ventral view of C. E, Medial view of anterior end of left premaxillary. F, Ventral view of E. G, Ventral view of posterior portion of left palatine. H, Medial view of the head of the right maxillary.

ones (Figure 7 A, B, E, F). The second tooth from the medial end of the bone in the outer row is about twice as large (at least in diameter) as the others. The bases of the two medial teeth are present on the fragmentary anteromedial end of the left premaxillary and most of the shaft is known from the right one. One or two more enlarged teeth may have been present at the anterior end of the premaxillary, but a total of more than three is unlikely.

Comparison: *Hoplopagrus* consistently has only a single row of smaller inner teeth, and usually has two enlarged canines anteriormost in the outer row of each premaxillary. The other recent snapper genera have a single outer row of canines with the anterior one to five teeth enlarged. The inner ones consist of two to five rows of villiform teeth, usually with more rows anterior and medial and less posterior and lateral.

Palatine: The small posterior fragment of the left palatine bears 12 small molariform teeth (Figure 7 G).

Comparison: This piece could have been from a palatine bone shaped like that of *Lutjanus*, *Ocyurus*, *Rhomboplites*, or *Pristipomoides*, but it is too fragmentary to discern the original shape. *Hoplopagrus* lacks palatine teeth and the bone is a narrow shaft without the wide flattened area which bears palatine teeth in other lutjanids.

Dorsal Spine Pterygiophore: The left side of the first dorsal spine pterygiophore and its two dorsal spines are exposed on a small chunk of limestone. The basal two-thirds of the moderately robust spines are present, and articulated with the pterygiophore. The pterygiophore is flat with a low, flat, straight ridge running ventrally from the articulation of the second spine. This ridge lies slightly posterior to a line vertically bisecting the lateral surface of the bone, and is slightly enlarged and rounded just ventral to the second spine base. Just ventral to the first spine, the pterygiophore bears a low, rounded protuberance which extends anterodorsolaterally. The length of the dorsal surface of the pterygiophore is about half the height of this bone; the ventral tip is broken and the height cannot be precisely determined.

Comparison: The lateral ridge below the second dorsal spine base, and the low protuberance below the first spine are of similar configuration in all the other snappers, except possibly that of *Pristipomoides* which was not examined. In the recent snapper genera the depth is two and one-half to four times the length of the dorsal edge, rather than about twice as in *Hypsocephalus*. The first two dorsal spines are slightly compressed, long and slender, and the first spine is just about half the length of the second in the recent snapper genera, and this appears to have been true for the fossil although only the proximal two-thirds to three-fourths of each spine is present.

DISCUSSION

The fossil resembles the living *Hoplopagrus guntheri* more than any other percoid examined. The living and fossil species together appear closest to lutjanids, although they are distinctive in their own right, and also bear

some resemblance to sparids and pomadasyids. This conclusion is largely (and necessarily) based on characters in the neurocranium and jaws, the only elements available in the fossil. The nature of the teeth on the premaxillaries, dentaries, vomer, and palatines has been stressed since they are often the only osteological features described for Indo-Pacific percoids (Weber and de Beaufort, 1931, 1936; Gosline and Brock, 1960; Smith, 1961; Marshall, 1964). Detailed search for relationships has been restricted to three families Lutjanidae, Pomadasyidae, and Sparidae. Comparative materials has been listed previously and the following works have also been useful: Gregory (1933); Patterson (1964); and Leccia (1961).

Characters taken together which distinguish the hoplopagrines² from other percoids are: 1) robust, conical teeth on the premaxillaries, dentaries, and vomer; 2) a vertical and transverse posterior facet on the basioccipital; 3) articular surfaces of exoccipitals for the atlas vertebrae not continuous across the midline; 4) a ventral, globular swelling on the posterior end of the parasphenoid; 5) a narrow, compressed otic region; 6) a strong, compact dorsal surface of the lateral ethmoids lateral to the anterior ends of the frontals; 7) lateral ethmoid facets for the palatine oriented as in lutjanids (see below); and 8) supraethmoid (not vomer!) convex in profile. Many of these characters are found elsewhere in percoids.

The robust conical teeth occur also among the lutjanids and sparids but show more variation in size in these families. In lutjanids the outer robust teeth are followed by minute villiform teeth, and the vomerine teeth are usually present and villiform. The only exceptions are some species of the lutjanid genus *Lethrinus* which have canines anteriorly and molariform teeth posteriorly (Weber and de Beaufort, 1936). Pomadasyids resemble lutjanids in having strong canines followed by fine villiform teeth, or having all jaw teeth villiform. Sparids all show considerable range of tooth shapes, with canines or incisors anteriorly and conical or molariform teeth posteriorly. The relatively uniform shape, lack of great dimorphism in size, the teeth diminishing in size posteriorly, and the presence of teeth on the vomer in hoplopagrines makes them similar to lutjanids.

The posterior facet of the basioccipital faces posterodorsally in pomadasyids and lutjanids. This facet is transverse and vertical in sparids as it is in hoplopagrines. In sparids the articular surfaces of the exoccipital facets accommodating the atlas vertebrae vary. Those of *Calamus* and *Archosargus* do not meet in the midline like those of hoplopagrines. They meet narrowly in *Lagodon*, and form a wide continuous surface in *Diplodus*. These facets meet through a continuous surface in lutjanids and the pomadasyids *Brachydeutereus*, *Orthopristis*, *Anisotremus*, *Haemulon aurolineatum*, and *H. sciurus*. They fail to meet middorsally in *Haemulon plumieri*. The hoplopagrines most resemble some sparids and some pomadasyids in the relations of the facets for the atlas vertebrae.

No development of a globular swelling at the posterior end of the para-

sphenoid is apparent in the lutjanids examined or in the pomadasyid *Anisotremus*. The remaining pomadasyids and all the sparids examined have such a swelling moderately to well developed. In contrast to the solid rounded protuberance of the hoplopagrines, the swelling in sparids and pomadasyids is bilateral with a midventral longitudinal groove partially dividing it. The hoplopagrines seem to resemble sparids and pomadasyids rather than lutjanids in possessing this swelling, but since it is differently formed in hoplopagrines it may be independently developed and not indicative of relationship.

All the lutjanids and pomadasyids examined have moderately to greatly inflated otic regions, but the hoplopagrines resemble the sparids examined in having a compressed otic region.

The size and arrangement of the cephalic lateral line system pores in hoplopagrines is within the range of variation seen in the lutjanids and sparids examined. The pomadasyids have distinctive large cephalic canals quite different from those in hoplopagrines.

The lateral ethmoids have a well-developed dorsal surface lateral to the anterior ends of the frontals in sparids and pomadasyids, and this surface is deeply excavated in all of the genera examined in these two families except in *Brachydeutereus* where the upper surface is only a shallow depression. In hoplopagrines this surface is rugose and flat or rounded as it is in lutjanids, although the surface faces largely laterally and slightly anteriorly in lutjanids rather than dorsally.

The orientation and position of the palatine facets on the lateral ethmoids of the hoplopagrines resemble those of all the lutjanids examined, namely one some distance behind the other with the anterior one slightly more dorsal and slightly more lateral than the posterior one. In pomadasyids the vomer and lateral ethmoid are longer and the facets are much closer together. The anterior one is directly anterolateral and slightly dorsal to the posterior one. The anterior facet faces much more laterally than in lutjanids as well. In sparids the anterior facet is strongly developed and faces anteriorly and slightly laterally, and the posterior facet is obsolescent. The supraethmoid is similar in size and shape in hoplopagrines and lutjanids, namely with a flat dorsal surface between the anterior ends of the frontals with a midventral keel anterior to this. The bone is convex dorsally in profile. In the sparids and pomadasyids examined the supraethmoid is concave in profile and is flat or excavated along the middorsal line, apparently to accommodate the long ascending processes of the premaxillaries.

In most of the characters shared by *Hoplopagrus* and *Hypsocephalus* and just discussed, the hoplopagrines resemble the lutjanids. A few characters like the swelling at the posterior end of the parasphenoid and the orientation of the posterior exoccipital facets resemble some sparids and some pomadasyids, but are differently developed or variably developed enough so that they do not seem to be strong indicators of relationship.

The characters in the dentition and ethmoid region of hoplopagrines are

probably the strongest evidence of a relationship with the lutjanids. The ethmoid region, maxillaries, and premaxillaries are basically similar and reflect the capability to expand the oral cavity both ventrally and laterally. The lutjanids, including hoplopagrines, are predaceous and have moderately protrusible mouths which also expand laterally, producing a large enough opening to utilize vomerine and palatine teeth which are present in most lutjanids. In both sparids and pomadasysids the mouth is restricted laterally, and the upper jaw is much more protrusible. These fish are largely nibblers and grazers (Randall, 1967), and the restricted lateral movement of smaller mouths has eliminated the need for vomerine or palatine teeth which are uniformly lacking in these two families. Thus, the hoplopagrines are interpreted as lutjanids which have retained the typical larger, expansive mouth, but have specialized to feed on resistant prey by developing strong, robust teeth resembling those of some sparids.

Hypsocephalus is distinctive among lutjanids in possessing two flanges on the prootic, one anterolateral and another posterolateral to the main columnar arch forming the anterolateral wall of the prootic. Sparids typically have two complete arches (Patterson, 1964) and I found this in all the sparids examined except *Lagodon* in which the posterior one is incomplete, resembling the posterior flange of *Hypsocephalus*. All the pomadasysids examined have a single complete arch with an additional free ending posterolateral flange from the shelf under the anterior prootic facet for the hyomandibular. More variation probably exists than has been suspected and this character should be investigated in as many acanthopterygians as possible.

Hypsocephalus is also unique among the lutjanids and sparids examined in lacking a pointed process on the epiotic just medial to the facet for the upper limb of the posttemporal. Among the percoids examined this process is lacking in all the pomadasysids, and the significance of this absence is not known.

The living *Hoplopagrus guntheri* has tubular anterior nostrils, a well-developed knob on the upper interopercle, thick, enlarged, and conical canines on the anterior ends of the dentaries and premaxillaries, conditions which cannot be determined in the fossil. Lutjanids generally possess the interopercular knob, but it is usually less well developed, and the sparids examined lack it. The sparids lack palatine teeth also, and the large canines and tubular nostrils are unique for *Hoplopagrus* among lutjanids and sparids. The lateral ethmoid canal for the olfactory nerve in *Hypsocephalus atlanticus* is about the same size as in other lutjanids, and it apparently did not have a particularly large nasal capsule, as does *Hoplopagrus* (Pfeiffer, 1964).

Lutjanids in general feed largely on crustaceans and fishes, with fishes forming a greater proportion of the diet in larger individuals (Randall, 1967). The strong molariform teeth of *Hoplopagrus* indicates that it eats resistant prey of some kind, as presumably did *Hypsocephalus atlanticus*. Edmund Hobson (personal communication) found *Hoplopagrus* to be nocturnal, and

believes that its feeding habits may be similar to a nocturnal Hawaiian sparid, namely *Monotaxis grandoculis* (Forskal). He finds this Hawaiian sparid to feed largely on hermit crabs and sea urchins which move out into the open more at night. Possibly the feeding habits of *Hoplopagrus* are similar, as perhaps were those of the fossil.

The description of the holotype of *Lutjanus avus* W. K. Gregory, 1930 shows that it consisted of a majority of the cranial bones, and they seem to be typical of the genus *Lutjanus*. *Lutjanus avus* had strong outer teeth and fine inner ones on the dentary and premaxillaries, and villiform vomerine teeth. Unfortunately the holotype of *L. avus* could not be found during a thorough search of the Florida Geological Survey Collections in 1957, (Stanley J. Olsen, personal communication), and thus it has not been re-examined.

The holotype of *Lutianus hagari* Jordan and Gilbert, 1919, recently transferred from Stanford University to the California Academy of Sciences, and the counterpart (LACM 1329), were examined and they do not represent a lutjanid as Jordan and Gilbert (1919) believed. The first four or five dorsal spines (11 in all) are longest. The next to the last four are about half the height of the anterior ones. The last spine is a little longer than these four and is very close to the much longer first soft ray, a condition found in percichthids, scorpaenids, percids, and some sciaenids, but not in lutjanids. The anal fin almost certainly had three anal spines, although the anteriormost small spine is difficult to distinguish. The posterior two spines are clearly marked, and the second is about one-third the diameter and about two-thirds the length of the third. A good number of cycloid body scales is present. The scale focus is placed posteriorly and six to nine radii occupy the anterior fields. The skull is badly crushed but at least the dentaries (and probably the premaxillaries) appear to have borne villiform teeth along with small canines.

The arrangement of dorsal spines and the cycloid scales definitely exclude the fossil from the family Lutjanidae. Percichthids (except *Stereolepis*) and percids are extremely unlikely in deep water Miocene deposits from California. All of the characters of the fossil noted above are found in *Stereolepis* and many scorpaenids, and upon thorough study the fossil of *Lutianus hagari* may prove to be one of these.

GEOLOGY AND PALEOECOLOGY

About fourteen and one-half meters of limestones ranging from Oligocene to Eocene in age occur within the measured stratigraphic section at Milton's Cave. The highest beds which outcrop at the surface are the marine Oligocene Marianna limestones about 3.5 meters thick. Under these are upper Eocene limestones which have been extensively studied (Puri, 1957; Cheetham, 1963). The Ocala group is the uppermost late Eocene bed, and the top of the Ocala group is represented by the Crystal River Formation. The Crystal River Formation is divided into an upper Bumpnose Member and a lower member. The skull of *Hypsocephalus atlanticus* was discovered in this lower member.

The lower member is also comprised of an upper and lower zone. The skull came from the upper zone which is a white to light brown, creamy, generally soft, granular relatively permeable and pure limestone. This zone is quite porous, has been carried into solution over large areas of the cave, and is called the *Operculinoides ocalanus-Asterocyclina* Zone by Puri and Vernon (1964). The two zones of the lower member are hard to distinguish and locally grade into each other.

The *Operculinoides-Asterocyclina* Zone indicates a depositional environment of a continental shelf region between 33 and 66 meters, with salinities from 32 ‰ to 37 ‰, water temperatures of 20°C or more, moderate agitation, and no evidence of reef formation (Cheetham, 1963; Puri and Vernon, 1964). Conditions found today between the continental shelf margin of Florida and the Bahamas Bank seem to be analogous with those which existed in the late Eocene, namely a gently sloping continental shelf bounded on the outside by a depression (Suwanee Straits of Eocene times) beyond which existed a bank (Ocala Bank of Eocene time). In the late Eocene, the mainland was in southern Alabama and Georgia and the highlands of central Florida were occupied by the Ocala Banks.

The specimen of *Hypsocephalus atlanticus* died and was deposited at moderate depths on a mainland shelf. The excellent three dimensional preservation indicated a relatively undisturbed bottom. A fish entombed in a sediment consisting of these fine foraminiferal particles may have been well preserved due to anaerobic bacterial action (Dunkle and Olsen, 1959). During late Eocene time the north Florida area was tropical or subtropical and the sea level was gradually falling (Cheetham, 1963). There was a progressive extinction of endemic forms among the cheilostome bryozoa (Cheetham, 1963), and the line of hoplopagrines snappers may have become extinct in the western Atlantic in this period as well. However, the Miocene, Pliocene, and Pleistocene also saw substantial sea level falls (although at progressively lower levels than the Eocene deposits) which were accompanied by cooling (Tanner, 1968), and the extinction of the hoplopagrines may have taken place at one of these later times. A tropical and subtropical shallow water reef shark genus, *Heterodontus*, was present through Miocene times in the western north Atlantic, but is known today only from the eastern Pacific, Indo-Pacific, eastern Atlantic and the Indian oceans. Both *Heterodontus* and *Hypsocephalus* may have been eliminated at the same time, when conditions in the Caribbean area apparently became unfavorable for warm water forms living about hard substrates at shallow and moderate depths.

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